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DEMOGRAPHY OF NATURAL AND REINTRODUCED POPULATIONS OF *ACANTHOMINTHA DUTTONII,* AN ENDANGERED SERPENTINITE ANNUAL IN NORTHERN CALIFORNIA

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ABSTRACT

The purpose of this study was to 1) demographically monitor the only remaining natural population of the rare serpentinite annual plant *Acanthomintha duttonii* (Lamiaceae); 2) attempt to reintroduce a new, experimental population within historic range; and 3) evaluate the new population by comparing its demographic characteristics with those of the natural population. The natural population of *A. duttonii* at Edgewood Park significantly and progressively increased in abundance and density between 1990 and 1994, then began a decline that lasted through 1997. In general, high density and high yield (reproductive plants produced from previous year's nutlet production) were associated with average or below-average years of precipitation while low densities and yields were associated with above-average rainfall years. During the entire study period, survivorship to reproduction remained fairly high and consistent, indicating that population trends were due to variations in nutlet production and the influence of cryptic factors that operate in the seed bank. The experimental population at Pulgas Ridge differed in several critical respects from the natural population, including low germination, low and variable survivorship, low nutlet production and perhaps high nutlet mortality. These features reduced the potential for self-sustained growth in the experimental population, which is likely to be extirpated within the next few years. This failure to produce a self-sustaining population of *A. duttonii* emphasizes the urgent need for in situ preservation of self-sustaining natural populations of serpentinite species.

Serpentinite endemics comprise the largest single edaphic category of rare plants in the native flora of California (Pavlik and Skinner 1994). They tend to occur in low elevation grassland and chaparral habitats on rocky outcrops, gravel colluvium and alluvial clays throughout the California Floristic Province, especially in the coast ranges and Sierra Nevada foothills (Kruckeberg 1984; Fiedler 1992). These same localities are also favored by land developers who build houses at the edges of rapidly expanding cities. The increasing development pressure on serpentinite habitats requires more effective conservation strategies if we are going to maintain these species as wild populations in California. Among those strategies are the preservation of remaining natural populations on managed reserves (Reznicek 1987; Lessica and Allendorf 1992; Pavlik 1996) and the creation of new populations within historic range (i.e., reintroduction) to decrease the overall probability of species extinction (Pavlik 1994; Guerrant and Pavlik 1997). Reintroduction has also been used in a mitigation context, attempting to ameliorate the destruction of natural populations by transporting propagules onto protected sites. Reintroduction in any context is fraught with difficulties and uncertainties (see Falk et al. 1996), but is especialy so when conducted under the fiscal, temporal, and political constraints imposed by mitigation (Howald 1996).

The San Mateo Thornmint, *Acanthomintha duttonii,* is among California's most endangered plant species (York 1987). This state- and federally-listed plant occurs in a single, fragmented population at Edgewood County Park on the San Francisco peninsula (Sommers 1984; Skinner and Pavlik 1994). The population has a particularly high risk of extinction because of its small areal extent, proximity to high density suburbs and altered water runoff patterns from upslope development. Once a popular spot for off-road motor vehicle recreation, the site now experiences only sporadic disturbance by hikers and mountain bikers.

Other than being an annual plant restricted to serpentinite grasslands, relatively little is known about the demography, ecology, and genetics of *A. duttonii.* No demographic monitoring (*sensu* Pavlik 1987; Pavlik and Barbour 1988; Pavlik 1994) has been conducted on this or any other species of *Acanthomintha.* Surveys of *A. duttonii* at its only remaining natural population have recorded large fluctuations in population size. In 1984, fewer than 5000 individuals were found, while estimates in 1981 and 1986 were closer to 3000 (Sommers 1986; CNDDB 1989). An apparent high of 6000 during 1985 was reported by McCarten (1986). Although such fluctuations are to be expected in populations of annual plants, the responsible factors have yet to be identified and related to management of this endangered species.

The purpose of this study was to 1) institute demographic monitoring to determine general trends and limiting factors in the only remaining natural population of *A. duttonii* at Edgewood County Park, 2) attempt to reintroduce a new, experimental population within historic range and appropriate habitat, and 3) evaluate the new population by comparing its demographic characteristics with those of the natural population.

Materials and Methods

Study Species and Study Sites

The most recent taxonomic treatment of the genus *Acanthomintha* (Lamiaceae) has been done by James Jokerst for the Jepson Manual (Hickman 1993). He recognized four species (*A. ilicifolia, A. obovata, A. duttonii,* and *A. lanceolata*) on the basis of style morphology, corolla morphology, stamen fertility, leaf morphology, geographic distribution, and substrate preference (Jokerst 1991). *Acanthomintha duttonii* is an annual, frequently unbranched herb with dense glomerules subtended by spineless bracts (in contrast to the spine-tipped cauline leaves). The bilabiate corolla is white or tinged with lavender and contains 4 stamens with reddish anthers. Each flower is capable of producing a maximum of 4 nutlets.

Nothing is known about the genetic structure of the population. *Acanthomintha duttonii* is primarily a self-pollinating species (Steeck 1995), although visits to the corolla by small insects are frequent during the spring. As inferred from electrophoretic studies of other inbreeding plants, intrapopulation allelic variation would probably be relatively low and interpopulation variation would have been high prior to extirpation (Hamrick et al. 1991). This pattern is typical of habitat specialists whose populations are isolated from each other by significant barriers to gene flow.

Ecologically, *A. duttonii* is restricted to mesic serpentine grasslands that receive an average 500 mm of precipitation per year. At Edgewood Park, site of the only remaining natural population, mean annual temperature is 15°C with a mean annual temperature range of 11.1°C. Frosts are rare, with freezing temperatures occurring in less than 0.5% of the hours of the year (estimated from a Bailey nomogram). It is associated with more widespread grassland dominants, such as *Nasella pulchra, Lolium multiflorum, Delphinium hesperium* and *Hemizonia congesta* var. *luzulifolia* (nomenclature follows Hickman 1993).

McCarten (1986) conducted detailed surveys of actual and potential habitat of the species in San Mateo County. He did extensive soil sampling and found that the deep serpentinite clay of the Edgewood site was moist, chemically unusual, and rather uncommon in the county. Using these data and a wealth of field experience, McCarten and others (especially Susan Sommers, Toni Corelli and Ken Himes) mapped several possible sites for creating new populations. Pulgas Ridge, largely composed of serpentinite clay, lies along the eastern edge of the San Andreas Rift Zone and was identified as a general location suitable for reintroduction of *A. duttonii.*

The process of selecting microsites for new *A. duttonii* populations took many factors into consideration, including the ecological (macroclimate, soil, exposure, community associates, habitat size and degree of disturbance), and the logistic (land use history, road access, property ownership). A microsite on Pulgas Ridge was selected because of its apparently high quality habitat (mesic grassland on serpentinite clay soil), its public status as watershed lands operated by the San Francisco Water Department, and because it is very close to, if not within, the historic range of the target species. In many ways Pulgas Ridge resembles the Edgewood Park site, although its serpentinite areas are much larger and less fragmented by intrusions of non-serpentinite vegetation (e.g., oaks and annual grassland). The soil at Pulgas Ridge also compared favorably with soils at Edgewood Park (Pavlik et al. 1992) because it was found to be rich in clay (high saturation percentage) and chemically typical of local serpentinite (low nitrogen, low calcium/magnesium ratio, high nickel).

In addition to the ecological and logistic criteria discussed above, the microsite was selected to be; 1) large enough to allow a total of 24, 26 × 28 cm quadrats, separated by row and column spaces (access paths) 2) relatively homogeneous with respect to microhabitat factors (soil depth, slope, associated species, etc.), 3) accessible but reasonably concealed to reduce the potential for vandalism or other human disturbance, and 4) surrounded by suitable habitat so as not to constrain population growth in the future. We chose an east-west trending channel of a small intermittent stream, with gently-sloping (25%) banks of serpentinite clay. Plant cover was relatively sparse and open and would not excessively shade or otherwise crowd the new *A. duttonii* plants.

Monitoring the Natural Population at Edgewood Park

Seedling density and survivorship to reproduction in situ. Estimates of adult plant densities in the natural population were made in May–June in the years 1990–1997. A total of thirteen 0.125 m^2 circular quadrats were used to map the population and to record the densities of other species (e.g., *Lolium multiflorum* and *Avena fatua*) on and off the serpentinite clay. Given the lack of security and high visitation at Edgewood Park, we decided to leave very few, cryptic markers for mapping locations within the population. Consequently, only five permanent quadrats were randomly positioned during May 1990 in the belief that more markers would have increased the probability of vandalism. An X-Y grid was superimposed on the population and used to determine the positions from coordinates generated by a random numbers table. In addition, eight transient quadrats were distributed around the permanent quadrats at that time, increasing the number of density estimates for our maps. In following years, the locations of transient quadrats were approximated. After flooding had promoted downslope colonization during the winter of 1991–1992, two new permanent quadrats were established. The quadrats were used to determine the mean density of reproductive plants and to estimate total population size (when multiplied by the area of the population, about 42 m^2).

The same permanent plots were also used to estimate survivorship to reproduction during the 1991 to 1997 growing seasons. Fifty seedlings of *A. duttonii* were marked within each permanent plot when germinules were at the 4–6 leaf stage (January–February). The plots were revisited in June and the number of marked, reproductive plants were tallied.

Plant size and nutlet production. During peak flowering period (May–June) of 1990 to 1996, whole plants of *A. duttonii* were non-randomly selected to represent the complete range of plant sizes within a variety of microhabitats. These plants were clipped at ground height, sealed in individual bags and taken back to the laboratory. Stem length was measured from the clipped point to the base of the lowest glomerule. Forty-three plants were collected in 1990 and 25 plants were collected in each of the following years. Correlations between stem length and reproductive output were established using methods developed during studies of other endangered plants (Pavlik and Barbour 1988; Pavlik et al. 1993). Linear and non-linear models were applied to the data in each year, but the former produced higher correlation coefficients in most years and was, therefore, consistently applied across all data sets.

In June of each year, all plants that survived to reproduce within the permanent survivorship quadrats were measured for stem length and number of glomerules. These parameters were used to estimate mean plant size and nutlet output for the natural population and to generate frequency distributions of plant size for comparison with similar data collected for the experimental population.

Reintroducing the Experimental Population

Characteristics of the founder nutlets. The propagules (=nutlets) of *A. duttonii* used were collected from Edgewood Park in May–June of 1990 to 1994. Nutlets were taken from at least 40 individuals that represented the complete size range and microenvironmental amplitude of the natural population. The collection would be likely to contain, therefore, a representative sample of the existing genetic variation (Falk and Holsinger 1991). Nutlets were stored at 4°C in paper pouches within sealed plastic bags until they were sown in the field.

Laboratory germination trials were conducted in 1991 to 1993. Nutlets from each year's crop were tested the following January using three replicates of 25 nutlets each. A replicate consisted of a plastic petri dish (5.5 cm diameter) containing a filter paper disk that was kept moist with distilled water. Nutlets were spread across the paper disks and kept in a dark room in which the temperature averaged 25°C. Replicates were checked every day for 12 days, noting germination (protrusion of the radicle through the pericarp) and removing germinules with a paintbrush.

Installation. The population installed at Pulgas Ridge during the early winter of 1991 consisted of two sets of 12 plots each. A removable wooden frame containing a 7 × 7 grid of 49 holes was used as a template to precisely sow *A. duttonii* nutlets. The holes allowed exact placement and subsequent monitoring of germinules and juvenile plants. This "precision-sowing" technique has been successfully used by Pavlik and Manning (1993) to establish and monitor new subpopulations of the endangered *Oenothera deltoides* ssp. *howellii* and *Erysimum capitatum* var. *angustatum* and by Pavlik et al. (1993) to establish and monitor new populations of *Amsinckia grandiflora.*

In 1992 a total of 1176 nutlets of *Acanthomintha duttonii,* half from the 1990 crop at Edgewood and half from the 1991 crop, were sown into the 24 plots at Pulgas Ridge. Six additional precision-sown plots were established in the late fall of 1992. We also used a streak method for sowing five plots with 250 more nutlets on a small clay lens 30 m away from the stream bank. A linear furrow was cut in the soil with a blunt nail and sown with 50 seeds before covering it over with native soil. Streak plots did not allow for strict demographic measurements, but they were easier to establish and quicker to monitor. Additional enhancements to the reintroduced population were added in the falls of 1993, 1994 and 1995 in the form of ten more streak plots per year within 10 m of the demographic plots. All plots were sown in September–November of each year and no supplements of water or nutrients were applied. A summary of the nutlet inputs to all plots is presented in Table 3.

Monitoring and evaluation. The fate of each precision-sown nutlet was followed during the January to June growing season by repositioning the wooden frames on each plot and searching for seedlings. The condition of each seedling was recorded on plot-specific data sheets to allow calculation of critical demographic parameters (Pavlik 1994). Those parameters included field germination, stress factors (desiccation, etiolation, grazing by microherbivores), mortality, phenology, survivorship to reproduction, and plant size (number of glomerules and stem length). Streak plots were checked three times during the growing season for seedling emergence and each plant was measured at peak flowering period (May–June) for number of glomerules and stem length.

During the early summer of 1994, ten whole

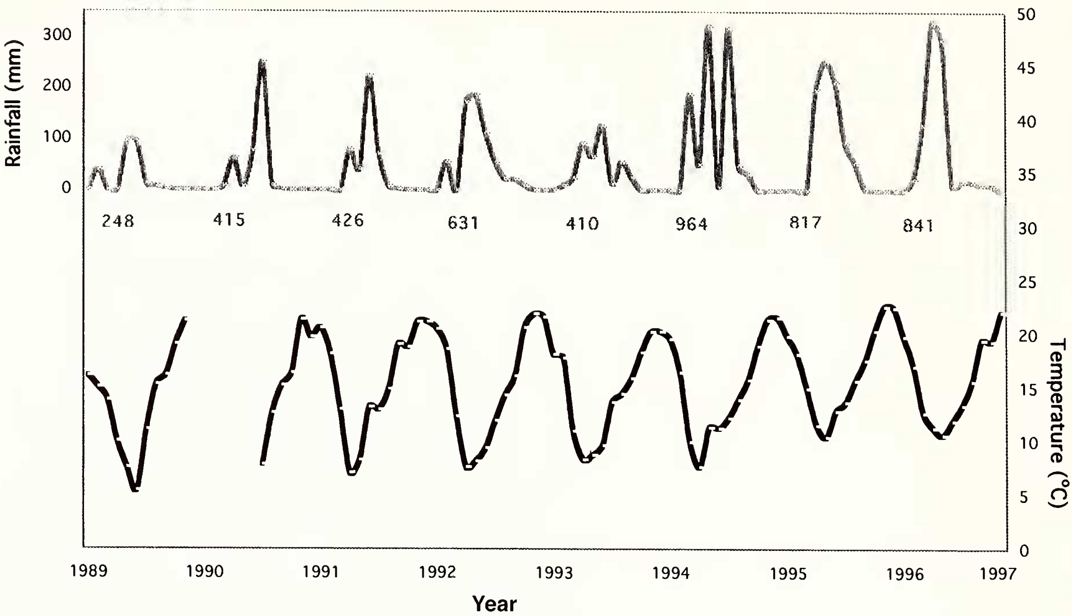

FIG. 1. Patterns of monthly precipitation and air temperature near the natural population of *Acanthomintha duttonii* at Edgewood County Park, 1990–1997. Rainfall totals for a growing season (November to November) are shown.

plants of *A. duttonii* were collected from the Pulgas Ridge experimental population. Stem length was measured from the clipped point (at soil surface) to the base of the lowest glomerule. Correlations between stem length and reproductive output were then calculated.

RESULTS AND DISCUSSION

Environmental Patterns 1990–1997

Rainfall varied significantly from year to year, but the seasonal patterns and magnitudes of mean monthly air temperature seemed to be similar for all years of the study (Fig. 1). Pronounced drought occurred during 1990 (November 1989–June 1990 growing season) when less than 300 mm was received in the vicinity of Edgewood Park. The years 1991, 1992 and 1994 were also dry relative to normal (about 500 mm), while 1993 was wetter than average. The years 1995, 1996 and 1997 were extremely wet, each exceeding 800 mm during the growing season. The overall pattern during the study, therefore, was one of low rainfall during the first five years (1989–1994) and extremely high rainfall during the last three years (1994–1997). Flooding of the natural population may have occurred during all wet years, but during the winter of 1991–1992 a single, intense storm had facilitated seed dispersal. This storm evidently caused soil erosion and downslope movement of nutlets into an adjacent patch of serpentinite clay that previously did not support *A. duttonii*. The newly-colonized area was subsequently included in the monitoring program. Flooding of some portions of the experimental population was prolonged during the extremely wet 1994–1995 growing season.

Another form of disturbance to the population was observed each late spring and summer. As the serpentinite clay soil dried and shrank, large surficial cracks began to open, sometimes as much as 4 cm wide and 30 cm deep. Mature nutlets would drop from adjacent plants into the gaping crevices. These cracks fill with water and clay during the next winter rain, perhaps burying a large number of nutlets at depths too great for seedling emergence. It is likely that these cracks significantly reduce potential population growth, but it is also likely that some nutlets remain viable for long periods of time within the seed bank. Observations made on a small, transient colony of *A. duttonii* in an adjacent portion of Edgewood Park have confirmed that nutlets can produce plants after 8 years of quiescence in situ. That quiescence, during which no adult plants were observed, was associated with high rainfall, *El Nino* climatic events during the early 1980's (Sommers 1986, Pavlik and Espeland 1994).

Demography of the Natural Population at Edgewood Park

Density and survivorship. During eight years of observation at Edgewood Park, mean density of the reproductive *A. duttonii* population could vary by a factor of 5 (Table 1), with a low of 230 plants/m^2 (1991) and a high 1106 plants/m^2 (1994). A 64% decline in density occurred between 1994 and 1995, with stepwise decreases through 1997. Spa-

TABLE 1. CHARACTERISTICS OF NATURAL AND EXPERIMENTAL POPULATIONS OF *ACANTHOMINTHA DUTTONII*, 1990–1997. Population size for natural population was estimated using the mean density and population area. Survivorship and density shown as means ± SD. Yield estimates were obtained dividing present population size by the previous year's nutlet production (Table 2).

	Emergence (%)	Reproductive survivorship (%)	Reproductive density (#plants/m2)	Reproductive population size (#plants/site)	Yield
Natural Population (Edgewood)					
1997	—	36.6 ± 11.5	63 ± 58	5289	0.128
1996	—	36.3 ± 12.1	89 ± 68	6885	0.126
1995	—	56.0 ± 32.7	390 ± 210	20,280	0.048
1994	—	52.0 ± 18.0	1106 ± 589	53,136	0.110
1993	—	62.9 ± 21.2	794 ± 756	36,279	0.305
1992	—	59.4 ± 29.4	302 ± 294	18,772	0.025
1991	—	54.8 ± 14.9	230 ± 78	9660	0.073
1990	—	—	689 ± 704	12,864	—
Experimental Population (Pulgas)					
1997	—	28.0	23	52	—
1996	—	39.0	35	77	—
1995	1.7	13.6	54	145	—
1994	10.9	53.2	66	158	—
1993	34.0	63.0	81	181	—
1992	27.0	38.0	68	120	—

tial variations in density were high (Fig. 2), with unique patterns found in each of the permanent plots. Patterns of increased abundance during drought years (Fig. 1), are supported by observations made on some species of common annual forbs (*Plantago erecta* and *Lotus subpinnata*) from serpentinite sites at nearby Jaspar Ridge (Armstrong and Huenneke 1992).

In contrast, survivorship to reproduction was fairly constant over time (~50%, Table 1) for the

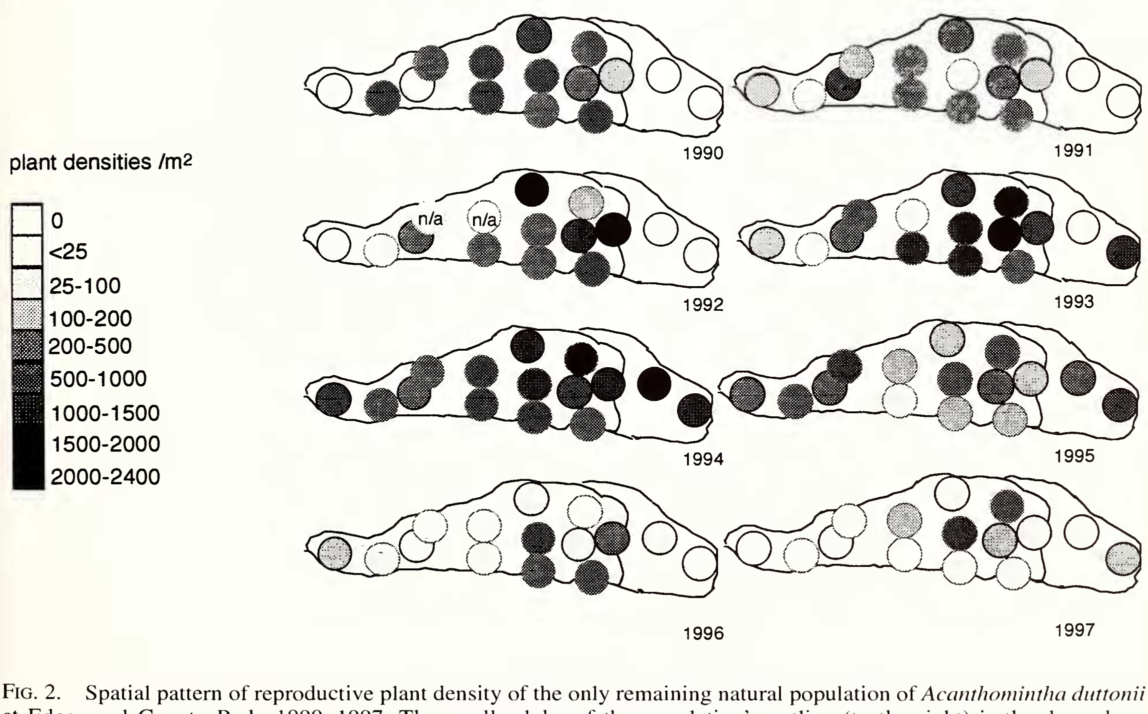

FIG. 2. Spatial pattern of reproductive plant density of the only remaining natural population of *Acanthomintha duttonii* at Edgewood County Park, 1990–1997. The smaller lobe of the population's outline (to the right) is the downslope addition colonized after flooding in the winter of 1991–1992. n/a = data not available.

TABLE 2. REPRODUCTIVE CHARACTERISTICS OF NATURAL AND EXPERIMENTAL POPULATIONS OF *ACANTHOMINTHA DUTTONII*, 1990–1997. Nutlet output estimated using #nudets/plant = m(stem length) + b. Nutlet production is the product of nutlet output and population size (Table 1). [a] = estimated using 1996 nutlet output correlation for the site [b] = estimated using 1994 nutlet output correlation for the site.

	Correlation between nutlet output (y) and stem length (x)					Mean plant size in plots		Estimated nutlet output	Estimated nutlet production
	m	b	r	P	n	Stem length (cm)	n	(#/plant)	(#/site)
				Natural Population (Edgewood)					
1997	—	—	—	—	—	4.1 ± 3.8	206	56[a]	3.0×10^5
1996	3.23	42.8	0.30	ns	25	5.3 ± 2.7	211	60	4.1×10^5
1995	3.51	8.1	0.39	<0.05	25	5.1 ± 3.3	198	26	5.4×10^5
1994	2.25	27.3	0.51	<0.05	25	4.0 ± 3.2	155	25	1.3×10^6
1993	2.86	36.1	0.45	<0.05	25	4.5 ± 2.4	220	49	1.8×10^6
1992	1.88	3.1	0.85	<0.01	25	6.9 ± 7.1	150	16	3.0×10^5
1991	9.00	−5.1	0.92	<0.01	6	9.2 ± 3.6	25	78	7.5×10^5
1990	2.83	21.1	0.71	<0.01	43	4.7 ± 2.5	188	34	4.4×10^5
				Experimental Population (Pulgas)					
1997	—	—	—	—	—	4.5 ± 3.4	55	30[a]	1560
1996	2.99	16.5	0.52	<0.05	15	9.4 ± 6.1	75	45	3375
1995	—	—	—	—	—	3.6 ± 2.8	145	27[a]	3045
1994	2.53	22.4	0.74	<0.05	25	5.2 ± 4.8	158	36	5688
1993	—	—	—	—	—	4.4 ± 2.5	181	34[b]	8869
1992	—	—	—	—	—	3.5 ± 1.5	315	42[b]	3150

population as a whole, tending to be slightly higher downslope in the newly colonized area and slightly lower upslope. Variations in plant density, therefore, are probably influenced by cryptic factors that operate in the seed bank (nutlet density, nutlet mortality, germination, emergence) rather than more obvious factors that control seedling growth and mortality.

Estimated total population size progressively increased from a low of 9660 reproductive individuals in 1991 to a peak of 53,136 in 1994. The ratio of reproductive population size to estimated nutlet production in the previous year (yield) was commonly between 0.07 and 0.13, with a single peak of 0.30 in the spring of 1993. The peak in population size was followed by a 60% decline in 1995, with no evidence of catastrophic flooding or anthropogenic disturbance. In years of decline there were intrusions of *Hemizonia congesta* var. *luzulifolia, Perideridia* sp., and *Lolium multiflorum* into the body of the population. Therefore, the recent decline in population size of *A. duttonii* appeared related to decreasing density across the entire habitat, with losses of potential habitat to common, serpentinite-tolerant species during especially wet years.

Plant size and nutlet production. The output of nutlets by individual *A. duttonii* plants in the natural population was linearly related to the sum of the stem lengths per plant in most years (Table 2). The slopes and intercepts of the relationship varied from year to year, but again there was no obvious correlation with environmental patterns or plant density. Mean stem length was greatest in 1991 and 1992 (years of below normal rainfall), but again there was no correlation between plant size and total yearly precipitation. Regardless of year, the large majority of plants in the population fell into the one glomerule or short-stem size categories and few were large and well branched (data not shown).

The total nutlet production of the population could be estimated using the nutlet output correlation along with estimates of mean plant size, population density, and population area for each year. Average plants usually output between 16 and 80 nutlets (Table 2), but the largest plants could make between 150 and 200 nutlets each. In June of 1992 an extremely large individual was found to produce 662 nutlets (from 232 flowers in 18 glomerules, with 66 cm of stem length in eight branches). Given the high density of the population in most years of the study, nutlet rain ranged between 10,300 nutlets/m^2 (1990) and 36,800 nutlets/m^2 (1993) (data not shown). Consequently, the total nutlet production of the natural population was in the range of 10^5–10^6.

Reintroduction at Pulgas Ridge

Laboratory germination of the founding nutlets. Nutlets of *A. duttonii* had moderate to high rates of germination in the laboratory. Germination averaged 87% for 1990 nutlets, 63% for 1991 nutlets and 71% for 1992 nutlets, even though all crops were approximately seven months old at the time the tests were conducted. There was a strong after-ripening requirement that prevented any germination during the six months following collection (June through December). Late winter germination appears to be characteristic of this species, owing to a rigid endogenous control mechanism that stratification, pericarp scarification, fire, wet-dry cycling, and red light cannot override (Pavlik and Espeland 1991). Perhaps such a mechanism prevents germination before a thorough saturation of the clay substrate takes place, thus avoiding the possibility of seedling desiccation during warm days in fall and early winter (also discussed in Armstrong and Huenneke 1992). Percolation is slower within clay substrates and so a higher proportion of the falling rain is likely to run off. Furthermore, clay particles require much more water than sands and gravels to bring soil water potentials into the tolerable range of −0.1 to −1.5 MPa for most seedlings.

Emergence in the field. Total emergence (in situ germination) during the late December 1991 to early April 1992 period was low compared to concurrent laboratory germination on the same seed lots. On average, only 27% of all sown nutlets emerged (Table 1), with the majority occurring by the end of January. In subsequent years, emergence was as high as 34.0% (1993) and as low as 1.7% (1995). It is likely, therefore, that nutlets remained dormant or died within the seedbank, and constituted a significant constraint on growth of the founding population.

Seedling establishment and mortality. A total of 315 live seedlings and established plants were found over the entire 1991–1992 growing season, corresponding to densities between 150 and 175 plants/m^2 (comparable to the natural population at Edgewood Park [Table 1]). Physical contact and shading between the seedlings and other plants were minimal because of the 1) virtual absence of annual grasses, 2) relatively large spaces between *Nassella pulchra* bunches and 3) the open or lax growth forms of the common herbs (e.g., *Perideridia kelloggii, Delphinium virgatum*) in this serpentinite grassland.

Despite this moderate production of seedlings at Pulgas Ridge, fewer than half survived to reproduce by early June 1992 (Table 3). Only 120 individuals completed fruit formation, or 38% of the total plants produced during the growing season and 10% of the total nutlets sown (the initial yield). Overall, survivorship to reproduction was low in the experimental population compared to that observed in the natural population at Edgewood Park. Mortality began early, with weekly mortality rates as high as 16.9% per week during the 28 January to 10 March period. The principle cause was difficult to identify from observations of grazing, desiccation, and etiolation stresses. Grazing by microherbivores (insects, snails, etc.) was the most commonly observed stress, affecting 4–34% of all live plants within plots during the growing season. Other stresses, including pathogens, may also be important during the early phases of population growth, but these were not assessed during this study.

TABLE 3. NUMBER OF NUTLET SOWN IN EXPERIMENTAL PLOTS (INPUT) DURING REINTRODUCTION AT PULGAS RIDGE AND THE NUMBER OF REPRODUCTIVE PLANTS SUBSEQUENTLY PRODUCED IN THOSE PLOTS AT PULGAS RIDGE, 1991–1995. Initial yield is the ratio of first year reproductive plants in spring to the number of nutlets input during the previous fall.

Fall input		Number of reproductive plants produced in spring				Spring initial
Year	Nutlets	1992	1993	1994	1995	yield
1991	1176	120	64	17	5	0.102
1992	514	—	117	29	4	0.228
1993	2000	—	—	112	25	0.056
1994	6450	—	—	—	111	0.017

Mean survivorship increased during 1993 and 1994 (63 and 53% respectively), but decreased to 13.6% in 1995. The decrease was caused by flooding in the ephemeral creek channel which inundated some of the reintroduction plots. Such large variation in survivorship, biased towards the low end of the range, characterizes the experimental population at Pulgas Ridge and not the natural population at Edgewood Park.

Plant size and nutlet production. Mean plant size at Pulgas Ridge in 1992 was less than that measured at Edgewood Park (3.5 ± 1.5 cm vs. 6.9 ± 7.09 cm), but only if the large colonizing plants of the natural population were included in the latter estimate (Table 2). Colonizing plants were those found downslope in a previously unoccupied, contiguous area (Fig. 2). By excluding the colonists, mean plant size of the introduced population compared favorably with that of the natural population (3.5 cm vs. 4.0 cm, respectively). During other years, mean plant size and nutlet output in the experimental population at Pulgas Ridge was comparable to those observed in the same years at Edgewood Park. Missing from Pulgas Ridge were the few, large, fecund individuals observed primarily as colonists in the new area at Edgewood Park. This indicates that although the general conditions for reproduction at Pulgas Ridge were suitable, they were not optimal. Perhaps optimal microhabitat patches do exist at the Pulgas Ridge reintroduction site, but they were not sown with nutlets during these reintroductions. Such patches can have a disproportional effect on population growth by producing a few, highly fecund individuals that generate hundreds, rather than tens, of nutlets each.

Persistence of reintroduced cohorts. Although the initial yields of reproductive plants could be as high as 23% at Pulgas Ridge (relative to the number of sown nutlets) and mean plant size was comparable to that of the natural population, none of the founding cohorts was able to increase in size during the study period (Table 3). Reductions in cohort population size between years were between 50 and 90% regardless of how the nutlets were sown (precision or streak) or the patterns of yearly precipitation (dry or wet). Despite a total input of more than 10,000 founding nutlets, fewer than 150 reproductive plants were found during the springs of 1995, 1996 and 1997. Again, we believe that post-dispersal factors, including high nutlet mortality and poor conditions for germination, were probably responsible. Even after a year such as 1994, when the natural population at Edgewood Park was flourishing, the reintroduced population was not able to increase its numbers. Progressive declines during unfavorable years with high rainfall indicate that the reintroduction of *A. duttonii* to Pulgas Ridge is unlikely to have conservation value or evolutionary potential and must be considered a biological failure.

We do expect, however, that germination from a declining but persistant seed bank at Pulgas Ridge will continue for a few more years. Ex situ studies have shown that nutlets of this species are long-lived (data not shown), and in situ observations have confirmed that nutlets can produce plants after 8 years of quiescence during periods of extraordinary annual rainfall. Perhaps the persistence of this population, as viewed from the standpoint of its ability to produce reproductive plants, is better judged by the long-term activity of the seed bank. If that seed bank were much larger (in the range of 10^5–10^6), the adult population produced even in unfavorable years might be enough to provide reproductive recharge. Collecting many nutlets from the natural population in order to boost the long-term activity of the seed bank may be another approach towards spreading the risk of extinction between multiple populations. If the Edgewood seed bank is as large as production measures indicate (Table 2), as much as 50% of the nutlet crop in a "good year" (e.g., total averaged 1.6 million in 1993/1994) could be harvested and transferred because the remaining crop would be equivalent to maximum production in a "bad year" (750,000 in 1991). The effects of harvest on the natural population would have to be monitored, but the very large existing seed bank should be able to buffer the impact for a few, non-successive years (Guerrant 1996). Careful spreading of these nutlets across the Pulgas site may also increase the probability of contacting optimal, but otherwise invisible, microsites that encourage the growth and persistence of the seed bank.

Conclusions

The natural population of *Acanthomintha duttonii* at Edgewood Park significantly increased in abundance and density during the 1990–1994 period. There were no strong correlations between density with overall temperature or precipitation patterns, but in general, high density and high yield were associated with average or below-average years of precipitation and the declines were associated with above-average rainfall years. Survivorship to reproduction remained fairly high and consistent, indicating that the trends were due to variations in nutlet production and the influence of cryptic factors that operate in the seed bank (nutlet mortality, germination). Nutlet production was in the range of 10^5–10^6 per year for the population as a whole and it is likely that the lens of suitable serpentinite clay habitat at Edgewood Park can become saturated with *A. duttonii* nutlets.

The experimental population at Pulgas Ridge differed in several critical respects from the natural population at Edgewood Park. First, the cryptic seed bank factors at Pulgas Ridge, especially low germination (emergence) and perhaps high nutlet mortality, may have placed a severe constraint on population growth. Secondly, survivorship to reproduction was more variable and more likely to be low at Pulgas Ridge. Finally, total nutlet production at Pulgas Ridge was on the order of 10^3 per year, even though plant size and nutlet output compared favorably with the natural population. These three features combined to reduce the potential for self-sustained growth in the experimental population. The reintroduction plots established in the winter of 1991 had 120 plants in the spring of 1992, but only 64 reproductive plants in 1993, 17 in 1994 and 5 in 1995. Similar patterns of decline in abundance were observed in the plots in all other years. It is likely, therefore, that the experimental population at Pulgas Ridge will be extirpated within the next few years depending on the activity of the seed bank. This failure to produce a self-sustaining population of *A. duttonii,* despite having taken great care in site selection, sowing and monitoring of the reintroduction, emphasizes the urgent need for in situ preservation of self-sustaining natural populations of annual serpentinite species.

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